

BREEDING BIOLOGY OF THE MONK PARAKEET

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ABSTRACT.—The Monk Parakeet (*Myiopsitta monachus*) is unique among parrots because it constructs stick nests rather than nesting in holes. This study provides a detailed description of the species' breeding biology and provides evidence that this species might breed cooperatively. Although many parakeet pairs were observed roosting in solitary nests, breeding occurred only in nests within colonies or chambers within compound nests housing other parakeets. The male was responsible for all or most of the nest construction and maintenance. He fed the female during the incubation and early nestling periods, but later in the nestling period both the male and female fed the nestlings. Most breeding attempts involved a male-female pair, but three separate breeding attempts were made by trios (two trios included a female and two males, and the third trio was composed of a male and two females). In the trios, one of the auxiliary bird contributed less to the breeding effort than the primary male and female. The observations of trios support the idea that Monk Parakeets are similar to cooperative breeders, but the lack of cooperation in nest building indicates that colonial nesting may be a result of other benefits of group living, such as improved predator detection. Received 7 Jan. 1998, accepted 16 Aug. 1998.

The social behavior of most parrots has remained unstudied, at least partly because of the difficulty of observing birds that are typically far-ranging and often dwell in forest canopies. Compared to most of its relatives, the Monk Parakeet (*Myiopsitta monachus*) is a relatively tractable species for behavioral study. It is common throughout its range, generally lives in semi-open habitat, and spends a large amount of time in the vicinity of its nests. Monk Parakeets are unusual among parrots for building large domed nests instead of nesting in holes (Forshaw 1989). These nests are built of twigs and may include several chambers, each occupied by a different pair or group of birds. Nests are often clustered in the same or nearby trees to form colonies, and they are used for roosting as well as for breeding (Forshaw 1989). In Bolivia, Monk Parakeets (*M. m. luchi*) build their stick nests on cliffs rather than in trees (Lanning 1991). The strong tendency to breed colonially, along with delayed breeding, reduced dispersal, and incidental helping led Bucher and coworkers (1991) to suggest that the Monk Parakeet breeding system shares some characteristics with cooperatively breeding species.

The large stick nests built by these parrots are the center of much of their daily activity.

They are used year round by breeding as well as non-breeding birds and, while building activity peaks during and immediately following the breeding season (Martella and Bucher 1993), maintenance occurs year round (Bucher et al. 1991). Nests are fully enclosed, domed structures, usually built using thorny twigs (Forshaw 1989). They typically include 1–4 chambers in natural settings, each with its own entrance tunnel (Bucher et al. 1991).

Pairs have been reported to be socially monogamous (Navarro et al. 1995), but the duration of pair bonds is unknown. Nestlings fledge approximately 40 days after hatching (Bucher et al. 1991) and remain with their parents for about three months (Martín and Bucher 1993). Martín and Bucher (1993) did not find any young with their parents in subsequent breeding seasons. However, Emlen (1990) found that in captivity offspring often continued to roost with their parents for up to two years after fledging. These grown young sometimes assisted their parents by bringing food to chicks and possibly incubating.

Work by Bucher and his collaborators (e.g., Bucher et al. 1991; Martín and Bucher 1993; Navarro et al. 1992, 1995) in Córdoba Province, Argentina, has yielded a great deal of information about the basic and population biology of these birds. Here I present the results of a detailed behavioral study of breeding Monk Parakeets. I examine the evidence that the species might be an incipient cooperative breeder, and that the compound nests com-

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monly built by Monk Parakeets represent an important form of cooperation.

METHODS

Study area.—During the Austral spring and summer (September–January) of 1993–1994 and 1994–1995, I studied the breeding behavior of Monk Parakeets in northern Entre Ríos Province, Argentina. The region receives approximately 1200 mm annual rainfall (Rojas and Saluso 1987), mostly during the spring and summer months (A. Ortíz Basualdo, unpubl. data). Mean annual temperature is approximately 19° C, with summer (January) and winter (July) means of 26° C and 12° C, respectively (Rojas and Saluso 1987).

My study area encompassed an approximately 1000 ha uncleared portion of Estancia Santa Ana de Carpinchorí (58° 45' W, 31° 25' S), a 5508 ha cattle ranch near the town of Federal. Parts of Estancia Santa Ana have been cleared, but much of it is savannah woodland, dominated by three xerophytic trees: *Acacia caven*, *Prosopis affinis*, and *Prosopis nigra*. Additional trapping of birds was done at Estancia Palmira, a 4974 ha ranch that adjoins Estancia Santa Ana. During the years preceding 1992, parakeets on the ranches had been subject to annual control measures (poisoning and burning of nests) that are required by law in the area. These control efforts were suspended 1992–1995 throughout the study.

Observations.—At the beginning of each field season, I located all nests in the study area by riding through the area on horseback and interviewing the ranch hands. Throughout the season, I monitored the occupancy and breeding activity of all nests that were accessible with a 7-m ladder.

Observations (2–3 hours every 3–4 days) were initially made at all nests to select focal nests, which were those occupied by birds that showed signs of breeding. Focal nest observations were made at three day intervals (mean = 3.0, \pm 1.08 SD days) in 1993–1994, and every 3.2 \pm 1.29 days in 1994–1995. Each focal nest observation lasted an average of 220 \pm 58 min in 1993–1994 and 147 \pm 15.5 min in 1994–1995. Nests that were used primarily for roosting (i.e., birds were seen there only early in the morning and late in the afternoon) were visited less frequently. I increased the frequency of observations if the birds showed signs of breeding. I made observations for a total of 606.25 h in 1993–1994, and 623.75 h in 1994–1995, with 305 h and 491.5 h respectively focused on nests of breeding birds.

I followed a rotating observation schedule so that the time (early morning, mid-morning, early afternoon, mid-afternoon) of observations was varied systematically for all nests. Weather permitting, observations began at sunrise and continued until middle or late afternoon (16:00–17:00 local time). All observations were made from 15–30 m away (birds quickly became habituated to me), with the aid of 7 \times 35 binoculars and/or a 15–45 \times 60 zoom spotting scope. The activity and location of all focal birds (2–6, depending on the

number of pairs breeding in the focal nest or nests) were recorded every two minutes in a notebook, along with other observations (e.g., arrivals and departures, aggressive and affiliative interactions, building activity, etc.). While observing focal birds, I recorded the size of groups (including “groups” of one bird) that flew past, and also recorded the sizes of groups seen while I rode to or from observation sites. Observations were suspended during rainstorms because the birds did little more than sit. Observations were not made at nests whose occupants I had attempted (successfully or unsuccessfully) to trap on the previous night.

Only breeding males' and females' nest building are compared here. I quantified nest building and maintenance in three ways: number of twigs added per hour, number of minutes per hour spent adjusting/rearranging twigs, and number of minutes per hour spent shredding twigs. This final activity involves chewing twigs into small pieces that are used to line the nest chamber. Although I usually couldn't observe the activity, it was clearly audible. To avoid pseudo-replication, I pooled breeding attempts for pairs that were observed during more than one attempt, thereby yielding one set of data per breeding pair.

For the time-budget analyses of breeding behavior, the observations from multiple breeding efforts were similarly pooled, and trios were excluded from the analysis. Time-budget estimates were broken down into three time periods: pre-laying (the 10-days prior to clutch initiation), laying, and post-laying (the 10 days following completion of egg-laying). In calculating the proportion of time that the male and female were together, I assumed that the pair was together only if I saw them leave and arrive together. The female was considered to be alone only if I knew where she was and knew that the male was gone, or vice versa. If both were gone from the nest area, but left and/or arrived at different times, the time interval was excluded from the analysis. Individuals were considered to be in the nesting area if they were within 100 m of the nest.

Trapping, marking and sex identification.—Parakeets were trapped at night as they roosted in their nests, using a modified, light-weight version of the trap designed by Martella and coworkers (1987; see Eberhard 1997). Captured birds were held overnight in numbered cloth bags. At daybreak they were banded, weighed, and a blood sample (approximately 50–100 μ l) was taken from the brachial vein. The blood was immediately placed in 1.25 ml of lysis buffer (0.1 M Tris, 0.1 M EDTA, 2% SDS, pH 8.0) and later frozen. Colored anodized aluminum leg bands (Gey Band and Tag Co.) were used to mark the birds for individual identification. Immediately after being processed, birds were released within 300 m of their nests. To avoid disturbing birds that were in the process of settling into a nest, individuals sometimes were temporarily marked using dyes (Rhodamine B or Malachite Green, Sigma Chemical Co.). This was accomplished by mixing a saturated dye/alcohol solution with petroleum jelly; the dye-impregnated jelly was then dabbed on the nest en-

trance and birds dyed themselves as they passed through the opening.

Because Monk Parakeets are sexually monomorphic [Forshaw 1989; or "similar" according to Juniper and Parr (1998), who do not provide distinguishing characters], a sex-specific DNA probe (Zoogen, Inc.) was used to identify the sex of individuals in the study. The blood sample taken at the time of banding was used as a source of DNA, which was later extracted in the lab. Since the lab work was done after conclusion of each field season, behavioral observations were made without knowledge of the focal individuals' sex. Total genomic DNA was extracted from each sample and digested using a restriction enzyme (either TaqI or BamHI). Restriction digests were run out in agarose gels and transferred to nylon membranes by Southern blotting. Blots were probed by Zoogen, Inc., Davis, California to identify the sex of each individual. All the 1993–1994 samples were digested with TaqI, which revealed an alternate Z allele that made sex determination of some individuals ambiguous. For this reason, samples of those individuals' DNA were reprocessed using BamHI, which yields more consistent, dependable results. All of the 1994–1995 samples were digested with BamHI and no unusual alleles were detected. A more detailed description of laboratory protocols can be found in Eberhard (1997).

Nest checks.—Nest checks were begun once a female appeared to be incubating (i.e., once she began spending most of her time in the nest). The eggs were counted and a second egg count was made about 10 days later. At both of these egg checks, the eggs were numbered with indelible ink to facilitate the detection of future laying and egg disappearances. The nest was checked again when I estimated that all of the eggs should have hatched, and again about two weeks later, at which point the nestlings were banded and blood samples taken. Since Navarro and coworkers (1991) did not detect a negative effect of visiting nests every 10 days, I am confident that my less frequent visits did not adversely affect the breeding of birds in this study.

RESULTS

Sexes and weights of banded birds.—Eighty-five parakeets (56 adults and 29 nestlings) were banded at Estancia Santa Ana and another 50 (27 adults and 23 nestlings) were banded at adjoining Estancia Palmira. In the 1993–1994 field season, I attempted to trap and band all occupants of accessible nests at the start of the field season. During my second field season I trapped only focal birds, and did so only after the female had begun to lay.

Because the 1993–1994 sample of banded birds is a cross-section of the birds in the study area (not biased toward breeding pairs as the 1994–1995 sample is), it can be used as an indicator of the sex ratio of the adult

population in the Santa Ana and Palmira area. Of the 60 adult birds whose sex was determined, 30 were females and 30 males. The sex ratio of nestlings banded during both field seasons was almost equal: pooling the nestlings from both Palmira and Santa Ana, there were 27 females and 23 males. Weights of adult males (114.9 ± 7.19 g, $n = 37$) and females (114.8 ± 10.49 g, $n = 39$) were almost identical.

Nest locations.—During the two field seasons, I monitored 39 nests that were occupied for at least part of the study; I was unable to access 3 of them for regular nest checks, so they are excluded from the analysis of breeding behavior. The nests included 67 chambers (62 in the accessible nests), and had a mean of 1.8 ± 2.1 chambers per nest. Most of the nests that I monitored were built in *Prosopis nigra* trees, the tallest of the three native trees that dominate the study area. There were three colonies with nests built in the *Eucalyptus* sp. trees lining the ranch entrance, but only two nests from two of these colonies were included in my study because the others were too high to reach. One nest in the study was built on the cross-bar of a utility pole. Details about the sizes and locations of monitored nests are listed elsewhere (table 3.1 in Eberhard 1997).

Twenty-five nests were in colonies and 14 were solitary. Solitary nests are defined as those with nearest neighbors at least 100 m away. This definition follows from the distribution of nearest-neighbor distances shown in Fig. 1 and is consistent with Bucher's and coworkers' (1991) use of the term "colony", a term equivalent to Hyman's and Pruett-Jones' (1995) "nesting area." Nests from 7 colonies are included in the sample. While I use "colony" to denote a group of nests, it is important to note that each nest itself can contain several chambers. On two occasions I found more than one pair breeding in isolated multi-chambered nests and did not consider the pairs to be solitary breeders.

Nest building.—Nest construction and maintenance was observed throughout the breeding season by both breeding and non-breeding birds. Parakeets at Santa Ana used the thorny terminal twigs of three tree species common in the area (*Acacia caven*, *Prosopis affinis*, and *P. nigra*). Most of the twigs were clipped from trees within 100 m of the nest.

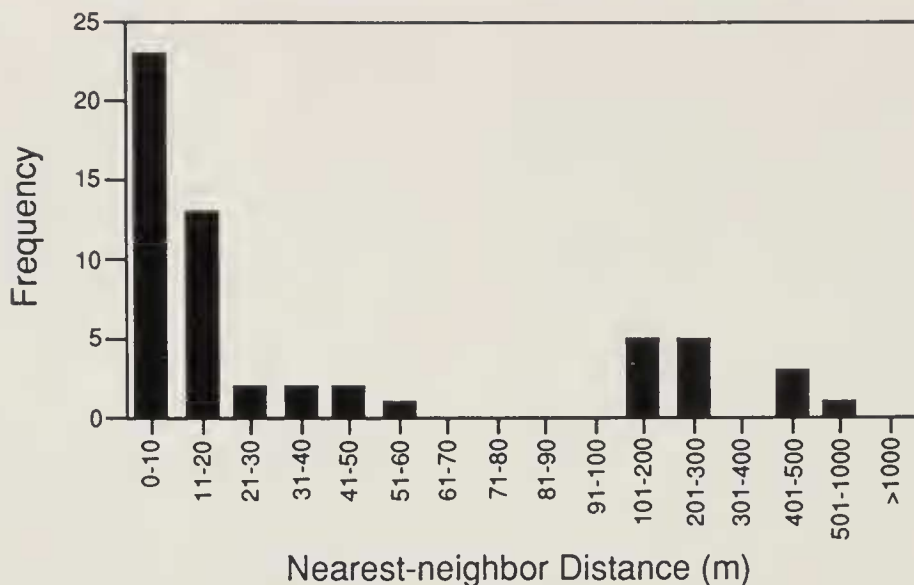


FIG. 1. Histogram of nearest-neighbor distances for all Monk Parakeet nests (both monitored and non-monitored; $n = 57$ nests) in the Santa Ana study area.

Some males stole twigs from neighboring nests or from parts of the compound nest away from the individual's compartment, often from occupied nests while the occupants were away. On average, 2% (range 0–8%) of the twigs added to nests were stolen ones. When building on a compound nest, twigs were always added to the individual's part of the nest; when adding to the roof, twigs were added only above the individual's chamber. Half of the 39 monitored nests had originally been built by Brown Cacholotes (*Pseudoseisura lophotes*) and subsequently remodelled by parakeets (J. Eberhard 1996).

The construction of new chambers often accompanied the initiation of a breeding attempt. Of 19 breeding attempts, 7 (37%) began with the construction of a new compartment. Only one of these new compartments constituted a new nest; all others were additions to existing nests. On four occasions, I observed pairs build a new compartment but not use it for breeding. Three of these four pairs moved out of their new nest (only one of these pairs was resighted later); the fourth continued to use the new compartment, but did not breed.

Males added more twigs than females (Wilcoxon test: $Z = -2.934$, $P = 0.003$, $n = 11$ pairs). Often, while the male was busy adding twigs to the nest, the female perched quietly nearby or inside the nest. When construction began, the female sometimes perched where the chamber would eventually be and the male

built around her. Males spent significantly more time adjusting and rearranging twigs on the nest (Wilcoxon test: $Z = -2.847$, $P = 0.004$, $n = 11$ pairs) than females. On the other hand, females spent significantly more time shredding twigs to line the nest chamber (Wilcoxon test: $Z = 2.032$, $P = 0.042$, $n = 11$ pairs).

The rate of nest-building (twig addition + twig rearrangement + twig shredding) activity was higher early in the breeding attempt. To test this, I compared nest building and maintenance rates during the 10-day period before egg laying began with the 10-day period after egg laying had been completed. Two breeding attempts by two different pairs were omitted from this analysis because no prelaying data were available for them. The mean percentage of time spent in nest building and maintenance during the prelaying period was 10.0% for males and 2.8% for females; during the post-laying period, these values dropped to 3.9% and 0.6%. Both males and females spent a greater proportion of time on nest-building and maintenance during the prelaying period compared with postlaying (Wilcoxon tests: $Z = -1.965$, $P = 0.049$ and $Z = -2.158$, $P = 0.031$, respectively; $n = 17$ breeding attempts). When pairs' multiple breeding attempts were pooled, this increased building effort was not detectable, possibly because of small sample sizes. In this pooled comparison, pre- and postlaying nest building and maintenance rates were not significantly different

for males or females (Wilcoxon tests: $Z = -1.580$, $P > 0.05$ and $Z = -1.660$, $P > 0.05$, respectively; $n = 10$ pairs).

Defense of the nest.—In general, Monk Parakeets were quite tolerant of having other birds (both conspecifics and other species) near their nests. During both breeding seasons, I observed 186 chases by members of breeding pairs. Males and females did not differ in the number of chases that they made (Wilcoxon test: $Z = 0.178$, $P > 0.05$, $n = 10$ pairs). On average, parakeets chased birds that were 3.0 m (± 3.1 m, $n = 186$ chases) from their nest, with no difference between males and females (Wilcoxon test: $Z = -0.700$, $P > 0.05$, $n = 10$ pairs). Other species were allowed closer (1.96 m) than parakeets (3.07 m) before being chased (Kolmogorov-Smirnov test: $D = 0.463$, $P = 0.011$, $n = 186$ chases).

The American Kestrel (*Falco sparverius*) and the Speckled Teal (*Anas flavirostris*) nested in Monk Parakeet nests at Santa Ana. Kestrel pairs took over two different compound nests during the study, and ducks nested in three of the monitored compound nests, using chambers that were not being used by parakeets.

Travelling groups.—When away from their nesting areas, parakeets generally traveled in small groups (mean = 2.98 ± 2.83 birds; range 1–30, $n = 777$ groups), but included more than one bird 87.5% of the time. As they left the nesting area, focal birds often joined other birds. I analyzed the departures of each focal pair separately (pooling multiple breeding attempts). In a total of 1893 departures by the members of 11 breeding pairs, over a quarter of the time ($27.1 \pm 10.1\%$) focal birds left the nesting area with other parakeets. On average, the groups they joined were composed of 2.0 ± 0.9 other birds. Neither the percentage of the departures that were with other birds, nor the size of departure groups, were correlated with the number of birds in the colony (Spearman rank correlation: $r_s = 0.243$ and $r_s = 0.178$, respectively; $P > 0.05$ for both cases).

Breeding groups.—Most of the breeding attempts I observed involved male-female pairs. However, on three occasions I observed breeding attempts by trios. Two of these included one female and two males, while the third trio was composed of one male with two

females. In the 35 nests (62 compartments) that I could access for regular nest checks, I observed 7 breeding attempts by 4 pairs and 2 trios in 1993–1994, and 12 breeding attempts by 8 pairs and 1 trio in 1994–1995. Of the six 1993–1994 breeding groups, four were followed in 1994–1995 also. At the beginning of the 1994–1995 field season, all four occupied the same compound nest they had occupied at the end of the previous season. In three of the four cases, the pair had moved to a new compartment. The other pair moved 600 m to a different colony following an unsuccessful breeding attempt in 1993–1994. The fact that the four breeding pairs followed during both seasons remained together suggests that Monk Parakeet pair bonds are long-lasting.

One 1993–1994 trio (a female with two males, FMM) disappeared from the study area after its nest was blown down by a storm during the incubation period. The other FMM trio was observed through the building, incubation, and nestling periods in 1994–1995. In both of these trios, one of the males (the “primary” male) was a more active participant in the breeding effort. During the incubation period, the primary male consistently went into the nest chamber after returning from an absence, presumably to feed the female; the auxiliary male returned less often, and usually sat outside the nest upon returning. Occasionally, the auxiliary male spent extended periods sitting in the nest with the female. Since I was rarely able to observe activity within the nest, I could not quantify the rates at which males fed females. However, on one occasion the female from one of the trios emerged from the nest and both males fed her. I observed little building by the first trio, and both males’ effort was approximately equal. Both males in the second trio collaborated in the initial construction of a new nest compartment, but later maintenance was all done by the primary male. One full-length copulation was observed between the two males in the first trio, who were 4 m from their nest in which the female was incubating.

The third trio (MFF) began its breeding attempt at the end of my 1993–1994 field season, so it was observed only during the building and incubation stages. All three birds participated in the construction of a new nest chamber that was quickly added to an existing

compound nest. One of the females (the “primary” female) assumed the task of incubating the clutch of 5 eggs. Once while the primary female was incubating, the male attempted to copulate with the auxiliary female 0.5 m from the nest but was rejected with lunges and biting.

Copulations.—Monk Parakeet copulations are prolonged and may include several mounts by the male. These series of mounts are best termed “copulation bouts” (Birkhead and Møller 1992). I observed a total of 31 successful copulation attempts and 14 unsuccessful ones. Following Snyder and coworkers (1987), a copulation attempt was considered successful if cloacal contact was clearly made. Because my observations were focused on nests, most of the copulations I saw were by the resident birds, but I observed a few copulations by non-resident birds, indicating that pairs also copulate away from their nests. The observed copulations occurred an average of 23 ± 79.2 m from the pair’s nest (range 0–410 m, $n = 44$ pairs). Six of the copulations took place inside nests and is likely an underestimate because it was difficult to observe activity within the nest.

Copulation bouts usually (33 of 45, or 73%) began with the male “head-shaking” (the bird ruffled up its head feathers slightly and gave its head quick shuddering shakes, raising its head slightly with each series of shakes) and sometimes strutted back and forth on his perch with very deliberate steps. Females would sometimes head-shake as well (18 of 45, or 40%). Males were more likely to initiate a copulation bout than females. Of 28 bouts in which one individual clearly initiated the interaction, 21 (75%) were initiated by the male. Occasionally the female mounted the male briefly as the copulation bout began. During his mounts, the male placed one foot on the female’s back and brought his tail under hers, bringing his cloaca against hers. All the while, the male waved his tail back and forth as he pressed his cloaca against hers and sometimes held his back open or gently grasped the female’s beak. The male usually dismounted a few times to head-shake or move to the other side of the female, so a single copulation bout often involved several different mounts by the male. Successful copulations often ended with the male pressing his cloaca more firmly

against the female’s for one or two seconds, after which he climbed off. In 16 copulation bouts for which I was able to determine which bird had terminated the copulation, it was usually (12 times, 75%) the male who simply stepped off. In four (25%) bouts, the female ended the copulation by putting her tail down or moving away. A successful copulation bout required the female’s cooperation, and clearly it was easy for her to end it; no forced copulation attempts were observed.

The average duration (from the beginning of the first mount to the end of the last) of successful copulation bouts was 274 seconds (range: 60–480 s, $n = 31$). In 19 of these bouts I measured the time that the male was actually mounted, as well as the total duration of the copulation bout. Males spent an average of 159 ± 53 seconds mounted (range: 30–263 sec, $n = 19$), which represents an average of 71% of the copulation bout (range: 47–100%, $n = 19$). Three copulation bouts included single mounts that ranged 60–120 seconds.

Mate guarding.—Because Monk Parakeets breed in colonies, they might be expected to engage in extra-pair copulations, and males to mate guard (Birkhead and Møller 1992). Comparing the percentage of time that the male spent with the female and the percentage of time the female was alone during the egg-laying period and the postlaying period, I found no difference in the proportion of time that the male and female were together (Wilcoxon test: $Z = -0.533$, $P > 0.05$, $n = 10$ pairs) or that the female was alone (Wilcoxon test: $Z = 0.561$, $P > 0.05$, $n = 10$ pairs) during the laying and post-laying periods. Therefore, there is no evidence that males guarded their mates during their fertile period.

Begging and allofeeding by breeding birds.—Egg-laying was accompanied, and often preceded, by an increase in the frequency with which females begged their mates for food. The females’ begging behavior was like that of young birds and often a begging call (see Martella and Bucher 1990) was given. Females were sometimes extremely insistent in their begging when the male was in the nest area. Adult males were never seen begging or heard making begging calls.

Begging by the female was strongly associated with egg-laying: the begging rate (min/h) during the prelaying and laying periods

TABLE 1. Breeding statistics for the 1993–1994 and 1994–1995 breeding seasons at Santa Ana (SA). Following Navarro et al. (1992), hatching success is defined as #nestlings/#eggs, fledging success is #fledglings/#nestlings, and breeding success is #fledglings/#eggs. Several clutches laid late in the season were not included in SA success calculations because they were due to hatch/fledge after the end of the field season: 93–94 (two clutches) and 94–95 (two clutches).

	SA 93–94	SA 94–95	\bar{x}_{SA}	\bar{x}_N^a	Range $_N^a$
# occupied chambers	27	29	28	52.1	38–78
% chambers with eggs	22.2	30.0	26.1	60.0	37–91
Mean size of first clutches	4.3	5.2	4.8	5.6	5.1–6.1
Hatching success (1st clutches)	0.3	0.6	0.4	0.6	0.5–0.7
Fledging success (1st clutches)	0.0	0.7	0.4	0.4	0.1–0.6
Breeding success (1st clutches)	0.0	0.4	0.2	0.3	0.04–0.4
% successful first clutches	0.0	62.5	31.3	43.7	14–53
% pairs re-laying	16.7	33.3	25.0	14.6	8–29
Mean size replacement clutches	4.0	5.0	4.5	4.6	4.0–5.1
Hatching success (rep. clutches)	0.0	0.2	0.1	0.4	0.2–0.5
Fledging success (rep. clutches)	0.0	1.0	0.5	0.4	0–1.0
Breeding success (rep. clutches)	0.0	0.1	0.0	0.2	0–0.4
% successful rep. clutches	0.0	50.0	25.0	29.0	0–67
Overall productivity per pair	0.0	1.8	0.9	1.5	0.5–2.3
Overall prod./occ'd chamber	0.0	0.6	0.3	0.9	0.4–2.0

^a Summary means and ranges of yearly means of data from a 7-year study of Monk Parakeets in Córdoba, Argentina (N; Navarro et al. 1992).

combined was significantly greater than the begging rate for all other times combined (Wilcoxon test: $Z = -2.803$, $P = 0.005$, $n = 10$ females). Males responded to this increased begging by increasing rates of allo-feeding (bouts/h). The rate at which males fed females was significantly greater before and during egg-laying compared with the allofeeding rate at other times (Wilcoxon test: $Z = -2.201$, $P = 0.028$, $n = 10$ males). Females were never seen allofeeding their mates.

Egg-laying and incubation.—Incubation began when the first egg was laid and was only by the female. During the laying and incubation periods, males returned every 1–2 hours, presumably to feed the female. Generally I was unable to observe activity within the nest chamber, but occasionally caught glimpses of or could hear the female being fed. On only two occasions (two different pairs) I saw the female emerge from the nest to be fed outside. Females sometimes left the nest during the incubation period to feed, to collect small twigs, to stretch, to chase away intruders, or because of a disturbance. Males spent time inside the nest during the laying and postlaying periods (16% and 24% of their time, respectively), but always with the female and did not appear to relieve her from incubation duty.

Care of the nestlings.—Females continued

to spend much of their time in the nest after the eggs hatched, leaving the nest more frequently and for longer periods of time as the nestlings grew. Since I was unable to observe activity within the nest chamber, and since both the male and female often entered the nest together, I could not quantify the feeding of young by males or females. It was clear that once she began leaving the nest, the female contributed to the feeding of nestlings. The nestlings usually fledged all at once, and thereafter spent little time in the nest. Most of the families with fledglings spent little time in the nest area (and when they did, were often hidden in the tree tops), so I was unable to observe many interactions between parents and offspring, and among offspring.

Breeding statistics.—Breeding in 1993–1994 began later than in 1994–1995, fewer pairs made breeding attempts, and none of those pairs was successful (Table 1). In 1993–1994, 22.2% of 27 the occupied chambers were used for breeding, and in 1994–1995 31% of 29 were used (this difference was not significant; $\chi^2 = 0.583$, $df = 1$, $P > 0.05$).

The mean clutch initiation date for 1993–1994 was 16 November, while the mean date for 1994–1995 was 26 October; this difference in clutch initiation date is not statistically significant (Kolmogorov-Smirnov test:

$D = 0.500$, $P > 0.05$, $n = 15$ first clutches). First clutches at Santa Ana contained an average of 4.8 eggs (range 3–7 eggs, $n = 15$); sizes of replacement clutches were not significantly different (4.5, range 3–7 eggs, $n = 4$ clutches; Mann-Whitney U -test: $Z = -0.300$, $P > 0.05$, $n = 19$ clutches). Overall, clutch sizes at Santa Ana tended to be smaller than those observed by Navarro and coworkers (1991; Table 1).

Hatching success (number of nestlings/number of eggs laid) for first and replacement clutches combined was significantly greater during the 1994–1995 breeding season than in 1993–1994 ($\chi^2 = 4.59$, $df = 1$, $P < 0.05$). Similarly, breeding success (number of fledglings/number of eggs; clutches due to fledge after the end of the field season were excluded) was significantly greater during 1994–1995 ($\chi^2 = 11.86$, $df = 1$, $P < 0.001$). Hatching and breeding success during 1993–1994, but not 1994–1995, at Santa Ana was lower than during any of the seven years of Navarro's and coworkers' (1992) study.

Predation and failure to hatch were the two most common causes of nest failure. Predation was never observed, but potential predators that were resident in the study area included snakes, opossums (*Didelphis virginiana* and *Marmosa agilis*), and kestrels. In all 4 cases of presumed predation, the nest itself was intact, and the adults were seen in the area later. The five complete hatching failures were restricted to two pairs, one of which was followed during both years. During the second field season, I opened or candled all unhatched eggs, and in the case of these two pairs, all unhatched eggs appeared to be infertile.

DISCUSSION

In their overview of Monk Parakeet biology, Bucher and coworkers (1991) suggested that Monk Parakeets show some characteristics that are typical of communally (i.e., cooperatively) breeding species. As outlined by Brown (1978), the most important feature of communal breeding systems is that helpers are regularly involved in the care and feeding of young. These helpers are generally individuals who defer breeding, so the evolution of helping behavior is "inextricably bound to the evolution of delayed breeding" (Brown 1978: 125).

Martín and Bucher (1993) found that Monk Parakeets delay breeding at least two years, and 50% wait longer. One of the most striking results from my study at Santa Ana was the finding that some breeding attempts involved trios. Emlen (1990) observed trios in a captive colony of Monk Parakeets, but the present study provides the first documentation of Monk Parakeet trios in the wild. While male-female pairs are the most common breeding unit, trios do not appear to have been an anomaly because they were observed during both years at Santa Ana. Bucher and coworkers (1991) observed incidental helping in the form of allofeeding: older fledglings fed their younger siblings, a non-breeding trio fed fledglings from a neighboring nest, and a breeding bird fed a begging juvenile from a neighboring nest. However, the low level helping observed in this study (like that observed by Emlen) occurred as a part of long-term associations that lasted through the breeding season. At Santa Ana both male and female auxiliary birds were observed assisting in nest-building and maintenance, feeding the incubating female, and possibly by watching for predators while they accompanied the incubating female. In the case of the trio with a female auxiliary, there was no evidence that she laid eggs; the group's clutch size was within the range of clutch sizes observed for other pairs in this study. The trios observed by Emlen (1990) involved a breeding pair's young (of unknown sex) from the previous breeding season. In the case of the Santa Ana trios, the identity and relatedness of the auxiliary to the breeding pair was unknown. Also unknown is the impact of the auxiliary bird's presence on the success of a breeding attempt.

A second form of helping described by Bucher and coworkers (1991) involves cooperation in the construction of nests, but my observations suggest that nest building was anything but cooperative. While the addition of a new chamber onto an existing nest appeared to facilitate construction, I did not see any clear cooperation among members of different pairs in nest-building. Twig theft (which sometimes involved an individual stealing twigs from areas of its compound nest away from its own chamber) was not unusual, and when building on a compound nest, an individual clearly focused its building on the

area of the nest immediately around its own chamber. Therefore, nest building does not appear to be a cooperative effort where various members of a compound nest collaborate to build a structure [such as the roof by Sociable Weavers (Collias and Collias 1984)] from which they all will benefit. Rather, multi-chambered nests seem to result from the convenience of adding chambers to existing nests compared with building nests from scratch.

The tendency for Monk Parakeets to nest in groups does not appear to result simply from attempts to reduce building effort by adding chambers onto existing nests. Most nests are small (<4 chambers), but built near one another in the same or adjacent trees. There is probably a trade-off between the benefits of reducing building effort and the cost of potential nest loss. Nests are typically built on the ends of rather thin branches, and large nests are more likely to fall during windstorms. Birds at Santa Ana showed a clear preference for breeding in colonies (no solitary breeders were found); solitary nests, which were often adopted cacholote nests, were used only as roosts (J. Eberhard 1996). My sample sizes were too small to examine the effect of colony size on breeding success. Navarro and coworkers (1992) did not find a statistically significant effect of communal nest size on productivity of a nest chamber. However, the grouping that occurs at the scale of colonies may be more important than grouping into compound nests, so a re-analysis of their data to examine the effect of colony size (instead of nest size) on productivity might be more relevant.

Potential advantages to Monk Parakeets breeding in colonies include increased ability to detect predators, group defense (Hoogland and Sherman 1976), and improved foraging efficiency (Ward and Zahavi 1973). Improved detection of predators could be especially important for incubating females because they are confined and cannot look out for predators. An approaching predator is announced with alarm calls by any parakeet in the area. Consequently, a female incubating in a colony is more likely to be alerted and leave her nest than a solitary female. This element of safety could explain the tendency of Monk Parakeets to breed in colonies rather than in isolated nests. The abundance and relatively uniform

distribution of food at Santa Ana during the breeding season (pers. obs.) suggests that colonial nesting is not likely to improve foraging efficiency. The lack of correlation between colony size and percentage of departures with other birds is consistent with this idea. In the autumn, when the parakeets earn their reputation as pests by descending on grain crops, food could be more patchily distributed and colonial roosting could hold a foraging advantage.

The most important correlate of breeding success found by Navarro and coworkers (1995) was laying date. Clutches laid early in the season were larger, produced more nestlings, and consequently more fledglings. This negative correlation between clutch initiation date and breeding success may explain the failure of pairs that attempted to breed during 1993–1994 at Santa Ana. The mean clutch initiation date that year was later than any of the mean clutch initiation dates recorded by Navarro and coworkers (1992) during their seven-year study at approximately the same latitude.

Although there are few detailed behavioral studies of wild parrots with which to compare this one, many of my observations appear to be typical of parrots. The finding that pairs persist for multiple breeding seasons fits the pattern of long-term pair bonds found in Puerto Rican Amazons (*Amazona vittata*; Snyder et al. 1987), the Galah (*Eolophus roseicapillus*; Rowley 1990), Spectacled Parrotlets (*Forpus conspicillatus*; Garnetzke-Stollmann and Franck 1991), *Agapornis* (Dilger 1960), and to some extent, Green-rumped Parrotlets (Waltman and Beissinger 1992). Incubation by the female and maintenance feeding of the sitting female by the male has also been reported for Puerto Rican Amazons (Snyder et al. 1987) and Galahs (Rowley 1990). Increased begging by the female associated with breeding has been noted in Yellow-shouldered Amazons (*Amazona barbadensis*; Sanz and Grajal 1998). In Galahs, head-bobbing (a component of begging) is part of the pre-copulatory behavior (Rowley 1990).

Monk Parakeet copulations are very similar to those described for *Agapornis* lovebirds (Dilger 1960) and Galahs (Rowley 1990). Compared with most birds whose copulations generally last less than 15 s (Birkhead and

Møller 1992), parrot copulations are remarkably long (range of mean durations: 30 sec. to >100 min.; Dilger 1960, Low 1992, Rowley 1990, Skeate 1984, Snyder et al. 1987, Waltman and Beissinger 1992, Wilkinson and Birkhead 1995). At least in the cases of Green-rumped Parrotlets (S. Beissinger, pers. comm.) and Thick-billed Parrots (D. Lanning, pers. comm.), copulations involved single mounts. The duration of Monk Parakeet copulation bouts, as well as some of the single mounts observed, are within the range of copulation times reported for other parrots. The function of these long copulations is not known, but they may be part of courtship (W. G. Eberhard 1996).

Monk Parakeets and species of *Agapornis* (which includes the only other parrots that construct nests) differ somewhat in their division of labor associated with nest-building and maintenance. In Monk Parakeets, the bulk of the nest building is done by males, and females shred twigs to line the nest cavity. In *Agapornis*, both cavity lining (in the species that don't build nests) and construction (in the nest building species) is the responsibility of females (Dilger 1960). This difference could be a result of the way in which nest building evolved in the two genera (Eberhard 1997). The construction of nests in the more recently derived species of *Agapornis* evolved from the habit of nest lining, which is done by the females of species that are basal in the *Agapornis* phylogeny (Eberhard 1998). A possible explanation for the male's predominant nest building role in Monk Parakeets is that this allows the female to conserve energy reserves for egg production.

In summary, the breeding behavior of Monk Parakeets is generally similar to that of other parrots for which comparable observations are available. The major differences are the nest building and maintenance associated with using stick nests instead of holes, the strong tendency to breed in colonies, and the occurrence of breeding trios. Further information about the frequency of breeding trios, the relatedness between breeding pairs and their auxiliaries, and genetic relationships between trios and their nestlings, would all be important in testing the idea that the Monk Parakeet mating system includes features that are characteristic of cooperative breeding sys-

tems. Though nest building itself does not appear to be cooperative, the construction of nests in lieu of nesting in holes probably permits individuals to form colonies. Roosting and breeding in colonies could in turn facilitate long term social associations throughout the year, allowing offspring to maintain close contact with their parents during subsequent breeding seasons and perhaps engage in helping.

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